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新疆的肯氏兽类新材料及短吻副肯氏兽的再研究[1)]

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摘要　记述了新疆吐鲁番中三叠统克拉玛依组肯氏兽类一新材料,它与短吻副肯氏兽(*Parakannemeyeria brevirostris*)正模特征相似,确定二者为同种。将中国已知的中国肯氏兽及副肯氏兽属的所有种进行支序分析,发现短吻副肯氏兽与中国肯氏兽及副肯氏兽属的其他种构成姊妹群。在与肯氏兽类其他相关属比较的基础上,建议以短吻种为基础建立一新属:西域肯氏兽(*Xiyukannemeyeria*)。

关键词　新疆吐鲁番,中三叠世,克拉玛依组,肯氏兽类

中图法分类号　Q915.864

新疆吐鲁番盆地桃树园沟为一丰富的二叠、三叠纪脊椎动物化石产地。上个世纪 60 年代野外考察期间在这一地区发现了塔尔朗组的古鳄类 *Turfania* (刘宪亭、马凤珍,1973),锅底坑组的二齿兽类 *Dicynodon* (孙艾玲, 1973; Lucas, 1998),韭菜园组的水龙兽(*Lystrosaurus*)(孙艾玲,1973)和加斯马吐龙(*Chasmatosaurus*)(杨钟健,1978),克拉玛依组的假鳄类 *Turfanosuchus*、*Vjushkovia* (杨钟健, 1973a, b)和迷齿类(杨钟健, 1966)(刘宪亭, 1973)。但在早三叠世晚期和中三叠世繁盛于世界各大陆的肯氏兽类却仅仅有一些头骨的碎片和零散的头后骨骼被发现。中科院古脊椎所 1983 年赴新疆考察时在这一地点的克拉玛依组找到了大量的肯氏兽类骨骼,为这一时期天山南北麓脊椎动物群的对比及与华北脊椎动物群的对比提供了补充依据。

在桃树园沟所发现的肯氏兽类骨骼,可能涉及近 10 个个体,其中以 83026(2)号标本(中国科学院古脊椎动物与古人类研究所标本登记号 V8311)保存最佳(图 1)。这是一具不完整的骨架,包括近于完整的头骨和下颌、右肩胛骨、右锁骨的近端、右肠骨和左右坐骨、部分脊椎、肱骨、右股骨、指(趾)骨等。

形态描述　V 8311 的头骨与产自天山北麓阜康县黄山街克拉玛依组的短吻副肯氏兽正模(IVPP V 4457)十分相似,包括纹饰这样的细微之处也是如此。

V 8311 头骨保存较完整,仅缺镫骨、牙尖。下颌右后部缺失少许。标本因受挤压而偏向右侧。头骨较大,长 364mm;最宽处在枕部,宽 208mm。头骨表面均分布着纹饰,但总体较光滑。

前颌骨较破碎,部分表面粗糙,可能是风化的结果,不是原始状态,其余部分均较光

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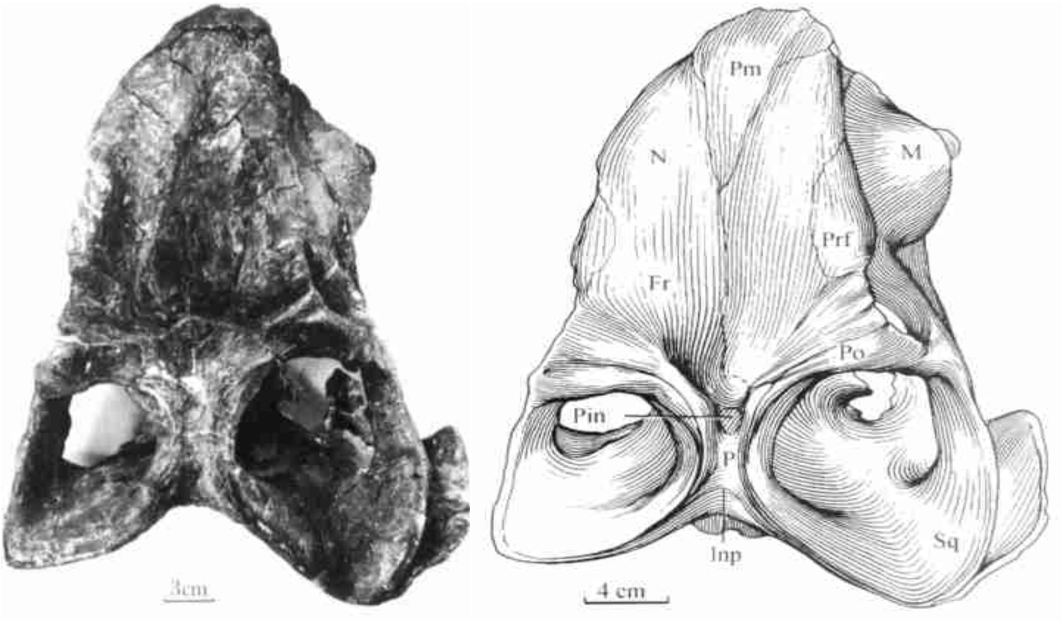

图1　短吻西域肯氏兽(新属)头骨顶视(IVPP V 8311)

Fig. 1　Skull of *Xiyukannemeyeria brevirostris* gen. nov. in dorsal view (IVPP V 8311)

简字说明 Abbreviations: Fr, frontal 额骨; Inp, interparietal 间顶骨; M, maxilla 上颌骨; N, nasal 鼻骨; P, parietal 顶骨; Pin, pineal foramen 松果孔; Pm, premaxilla 前颌骨; Po, postorbital 眶后骨; Prf, prefrontal 前额骨; Sq, squamosal 鳞骨

滑。吻部尖,无匙形凹面,但在最前端有一对小小的突起。前颌骨顶支与 V 4457 相似,也显得突起。吻部短而弯曲向下,眼前部仅长 140mm,为头长的 39 %。

上颌齿突肥大,扁而厚(图 2)。左侧齿尖已断,右侧仅存齿根,截面呈椭圆形,长径 21mm。由右侧齿可知其牙齿短小,向下方伸出。但上下颌咬合时牙齿超过下颌下缘。从右侧牙的断面上至少可以观察到三层同心环。上颌骨后支向后延伸接近眼眶后缘,与颧骨、鳞骨前支交错相接。

鼻孔很靠前,其后面是三角形的隔颌骨,此处较周围低凹。鼻骨表面有纹饰,侧视可见其在鼻孔后面部分有少许粗糙面。在 V 4457 上在鼻骨中间是下凹的接缝,而在这个标本上此处稍隆起,表明了鼻中脊的微弱存在。鼻骨和额骨的接缝呈 W 形。额骨前端中线部位稍隆起,在其两侧形成凹陷,W 的两个下角正位于此。左右额骨表面的纹饰对称,均为从其中后部向四周放射开去的条纹。

眶间区宽 141mm,顶视眼眶几不可见。眼眶大,长约 80mm,高约 30mm。眼眶前缘的泪骨为长三角形,向前延伸不与隔颌骨相接;眼眶上方的前额骨、额骨及后方的眶后骨的眶缘部分粗糙面发育。前额骨不突出,只有后外侧的少部分参与眼眶的构成。眶后骨向后延伸很远,与鳞骨相接触。颧弓前半段呈棒状,后半段横切面呈三角形。

前顶骨呈舌形,处在松果孔前的凹陷区。松果孔近圆形,开口向前上方。间颞部短而宽,不形成顶脊。间顶骨极前伸,顶骨异常短,这点与银郊中国肯氏兽(*Sinokannemeyeria yingchiaoensis*)相似。颞孔长大于宽,但由于变形难以确定其确切长度,估计从眶后骨后缘到鳞骨末端长约 130mm。

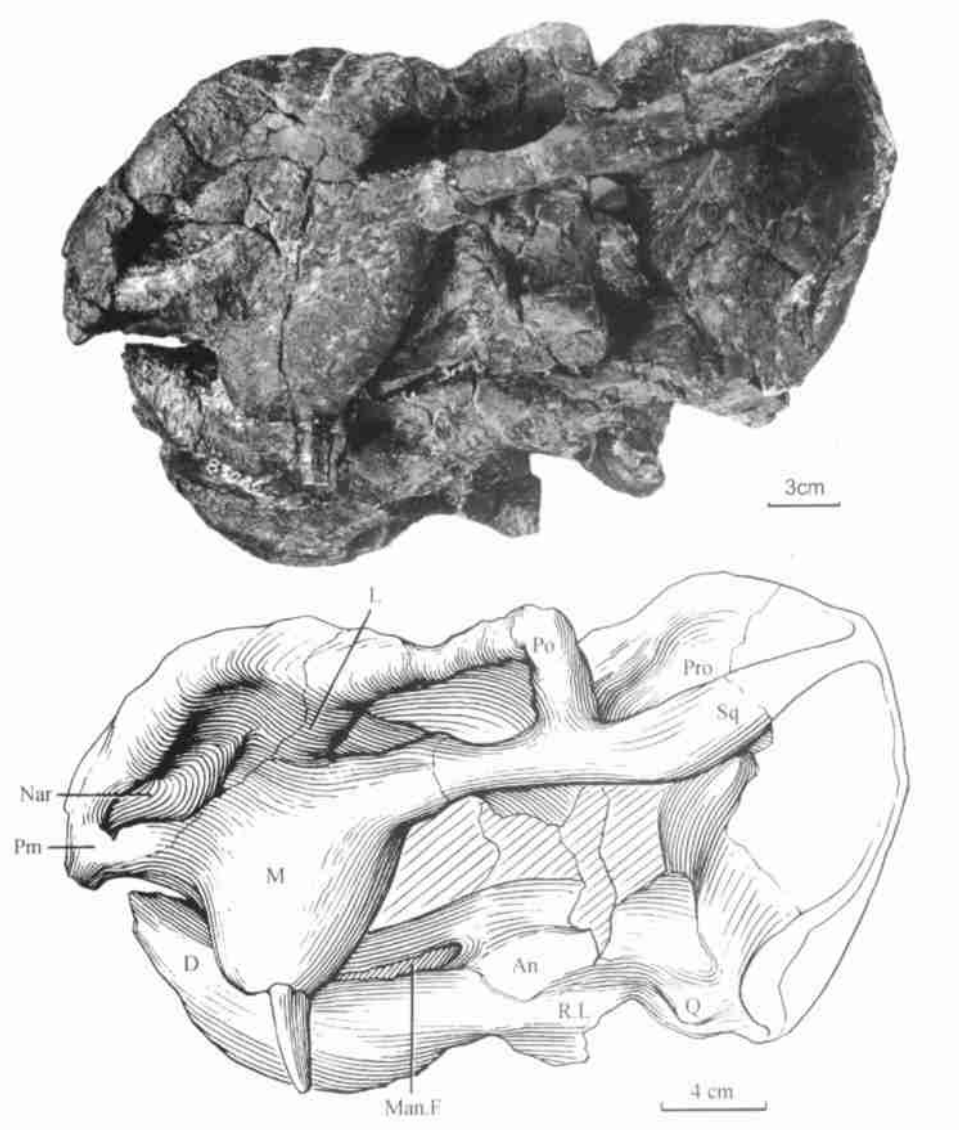

图 2　短吻西域肯氏兽(新属)头骨侧视(IVPP V 8311)

Fig. 2　Skull of *Xiyukannemeyeria brevirostris* gen. nov. in lateral view (IVPP V 8311)

简字说明 Abbreviations:An, angular 隅骨;D, dentary 齿骨;L, lacrimal 泪骨;M,maxilla 上颌骨;Man. F, mandible foramen 下颌孔;Nar, naris 鼻孔;Pm, premaxilla 前颌骨;Po, postorbital 眶后骨;Pro, prootic 前耳骨;Q, quadrate 方骨;R. L, reflacted lamina 隅骨外翼;Sq, squamosal 鳞骨

由于头骨与下颌紧紧地咬合在一起,故腹面前中部构造不能观察(图 3)。能看见吻部窄,前颌骨腹面为两脊夹一沟。从保存情况估计内鼻孔长约 50mm,翼骨间孔长约 10mm。颅基轴平直而宽短。基枕骨突起不太发育,它们之间的沟宽而浅。左侧的翼骨方骨支末端缺失,右侧被下颌掩盖。镫骨缺失。

枕面较平直,不甚宽大,枕高为枕宽的 59 %。鳞骨不太向外扩展。后颞孔周围的凹

图 3　短吻西域肯氏兽(新属)头骨腹视(IVPP V 8311)

Fig. 3　Skull of *Xiyukannemeyeria brevirostris* gen. nov. in ventral view (IVPP V 8311)

陷区大且深。枕髁宽 53mm ,高 39mm ,三分式明显 ,枕髁中央凹陷。其上的枕孔保存不佳(图 4) 。

下颌齿骨前端接近吻尖位置 ,关节骨的后部与上颌的方骨相关节。下颌长 260mm ,为头骨腹面长的 85 %。齿骨缝合部长约 98mm ,较粗壮 ,前腹部增厚 ,表面粗糙。齿骨上翼向后伸 ,覆盖了下颌孔上部 ,直达孔末端与上隅骨相接 ,下翼形成一角覆盖在隅骨前缘表面。下颌孔呈长椭圆形。隅骨外翼半耳状 ,宽而短 ,与关节骨相距较远。上隅骨前端被齿骨上翼盖住 ,下外侧被隅骨内翼掩盖。

表 1 列出了阜康标本 V 4457 和吐鲁番标本 V 8311 的头骨测量数据及各部之间的比例关系。这两个大小相近头骨的各部分比值也相差不远 ,只是吐鲁番标本的眶前部长度与头骨长度之比较阜康标本大 6 % ,而眶后部长度与头骨长度之比比后者小 6 %。

比较讨论　从上面描述可知 ,产自吐鲁番的 V 8311 与短吻副肯氏兽正模 V 4457 差异很小 ,它们都有短的吻部 ,牙短小 ,前额骨只有少部参与构成眼眶 ,颅基轴平直 ,枕髁明显三分。在头骨结构上二者之间明显的区别之一在于间颞部。虽然它们的间颞部都属短而宽的类型 ,但阜康标本间颞部向后稍向上升起 ,其构造和一般副肯氏兽相似 ,顶骨大部被

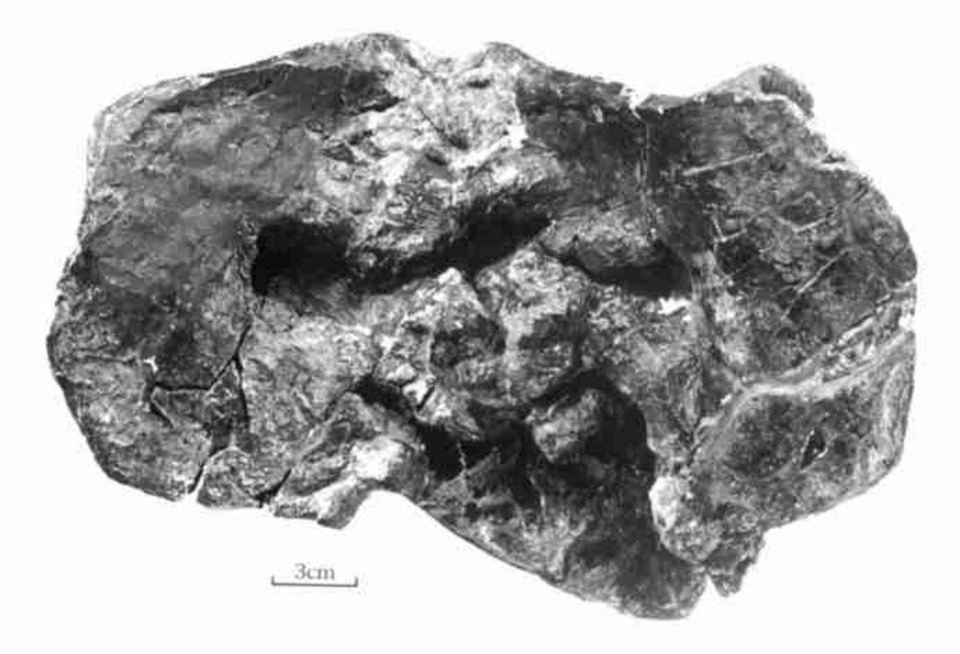

图 4 短吻西域肯氏兽(新属)头骨枕面观(IVPP V 8311)

Fig. 4 Skull of *Xiyukannemeyeria brevirostris* gen. nov. in occipital view (IVPP V 8311)

眶后骨覆盖,出露很少。间顶骨向前有较大的伸展,不过因为间颞部狭窄,只能伸出一个

表 1 阜康与吐鲁番头骨标本测量数据及比值

Table 1 Measurements and ratios of the skulls from Fukang and Turfan (mm)

	阜康标本 (V 4457)	吐鲁番标本 (V 8311)
头骨长度 length of skull	300	364
枕部宽 width of occipital plate	242	310
眶间距 width between orbits	119	141
眶前部长度 preorbital length	100	140
眶后部长(眼眶后缘—头骨末端) postorbital length	126	130
眶间距/头长(×100 %) width between orbits/skull length (×100 %)	40 %	39 %
眶前部长度/头长(×100 %) preorbital length/skull length (×100 %)	33 %	39 %
眶后部长/头长(×100 %) postorbital length/skull length (×100 %)	42 %	36 %
枕高/枕宽(×100 %) height/width of occipital plate (×100 %)	62 %	59 %

尖角。顶脊不像长头副肯氏兽(*Parakannemeyeria dolichocephala*)那样锐利,在正型标本上基本上是平的(孙艾玲,1978)。而吐鲁番标本椭圆形的顶孔在间颞部的位置更靠后一些。前顶骨自顶孔的前缘前倾,在两眶后骨之间形成一圆形的凹坑。由于头骨的这一部位稍有破损,前顶骨前缘的位置不清。眶后骨的主体部分粗大,在顶孔之后眶后骨呈一竖直的片状沿颞孔的内侧壁向后延伸,与鳞骨相接。与阜康标本不同的是,左、右两眶后骨在中线部位并未相遇,顶骨在顶孔之后两眶后骨之间有明显的出露,且中间部分下陷为宽而浅

的沟。间顶骨呈一舌状自枕部向前上方伸出,插入顶骨之内。这一结构与中国肯氏兽银郊种(*Sinokannemeyeria yingchiaoensis*)**的间颞部结构有些相似。**

二齿兽类(广义)的间颞部结构经常被用来作为划分属种的依据之一。已知资料证明二齿兽类同一属但不同种的动物的间颞部结构是存在差异的,但在其他特征一致的情况下仅间颞部不一致是否属于不同的种?根据阜康同一地点的肯氏兽个体观察,结论是否定的。V 4458 **包括保存在一起的** 9 **个个体,在这些标本中有两种不同结构的间颞部:其中** 1 **号的头骨与短吻种的正型标本结构相同——眶后骨覆盖顶骨,而** 2～9 **号头骨都由于顶骨出露,使间颞部呈凹陷(孙艾玲**,1978)**。后一种情况与吐鲁番标本**(V 8311)**一致。间颞部结构的差异并不妨碍将** V 4458 **和** V 4457 **归入同一种,同样吐鲁番的标本归于此种也是可行的。**

另外二者在鼻中脊构造上也存在差别:阜康标本(V 4457)**鼻骨中间是下凹的接缝,而吐鲁番标本则是较低的隆起,表明了鼻中脊的存在。在** V 4458 **中也有一个头骨**(No. 5)**可能与吐鲁番标本类似,但此头骨保存不佳,难以肯定。标本之间的这些差异可以解释为种内个体差异。**

孙艾玲(1978)**认为** V 4457 **与中国肯氏兽和副肯氏兽的关系较近,最后定为短吻副肯氏兽**(*Parakannemeyeria brevirostris*)**。另外中国肯氏兽与副肯氏兽还建立了** 8 **个种:皮氏中国肯氏兽**(*Sinokannemeyeria pearsoni*)**、银郊中国肯氏兽**(*S. yingchiaoensis*)**、三川河中国肯氏兽**(*S. sanchuanheensis*)**、长头副肯氏兽**(*Parakannemeyeria dolichocephala*)**、杨氏副肯氏兽**(*P. youngi*)**、宁武副肯氏兽**(*P. ningwuensis*)**、兴县副肯氏兽**(*P. xingxianensis*)**和神木副肯氏兽**(*P. shenmuensis*)(Young, 1937; Sun, 1960, 1963;**程政武**,1980)**。兴县副肯氏兽基于较破碎的头骨,被认为属于宁武种**(Sun et al., 1992)**。本文依据头部性状,对这些种间的关系进行分析(性状及矩阵见附录 Ⅰ、Ⅱ),分析时取二齿兽属** *Dicynodon* **作为外类群。**

用 Paup 4.0b10 **分析数据进行彻底搜索,得到一个最简支序图,其结果如图** 5 **所示。**

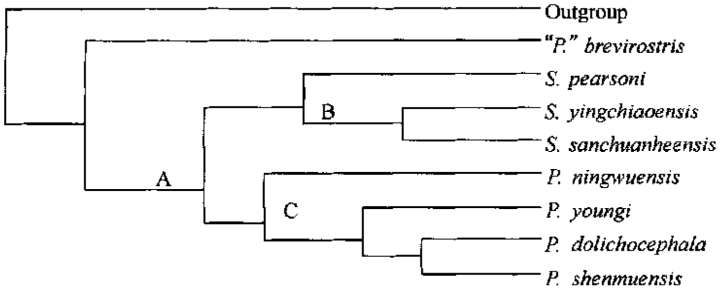

图 5 支序分析所得最简约树(**树长** 39,**一致性指数** 0.69,**保留指数** 0.74)

Fig. 5 The most parsimonious tree (Tree length = 39; Consistency index = 0.69; Retention index = 0.74)

用 ACCTRAN **辅助标准得到节点** A **的共近裔性状是** 4[1],6[1],7[1],9[1];**而节点** B **的共近裔性状是** 2[1],11[2],13[1],15[1],16[1],18[1],20[1];**节点** C **的共近裔性状是** 1[1],5[1],8[1],9[2],14[1];**而** *P. brevirostris* **的自近裔性状是** 3[1],5[1],11[1],13[1]。**用** DELTRAN **辅助标准得到节点** A **的共近裔性状是** 4[1],6[1],7[1];**而节点** B **的共近裔性状是** 2[1],9[1],11[2],15[1],18[1];**节点** C **的共近裔性状是** 1[1],5[1],8[1],9[2],

14[1];而 *P. brevirostris* 的自近裔性状是 3[1],5[1],11[1],13[1]。

新疆的短吻副肯氏兽与山西、陕西的副肯氏兽属有如下差别:眼前部非常短,前颌骨没有匙形凹面,牙短小,前额骨只有少部参与构成眼眶,眼眶较长,翼骨间孔小,枕髁三分明显,另外其间颞部比较宽,枕部稍宽,肱骨相对较短。它与中国肯氏兽也有较大差异。支序分析结果也表明新疆的短吻副肯氏兽应该从副肯氏兽中独立出来。

短吻副肯氏兽的头骨背中线长度与腹中线长度相当,按 Cox and Li (1983) 分类应归入 Stahleckeriidae 科,这个科除 *Parakannemeyeria*、*Sinokannemeyeria* 外还有 *Stahleckeria*、*Zambiasaurus*、*Dolichuranus*、*Rhinodicynodon*、*Dinodontosaurus* 等属。新疆的肯氏兽很容易与它们区分开来:前两个属无牙、无前顶骨、顶脊宽, *Dolichuranus* 吻尖方形、牙大、齿突小、前颌骨向后延伸至眼眶背面、有鼻中脊及鼻骨突, *Rhinodicynodon* 个体小、牙相对较大、有鼻骨突、顶孔小, *Dinodontosaurus* 吻尖方形、额骨仅仅很小一部分参与眼眶的组成、眶后骨不向后延伸、下颌隅骨外翼向后延伸接近关节骨。

根据 King (1988) 的分类, Sinokannemeyeriini 族有 *Dinodontosaurus*、*Uralokannemeyeria*、*Rhadiodromus*、*Parakannemeyeria*、*Sinokannemeyeria*。新疆标本与 *Dinodontosaurus* 的差别是前者头更弯更高,颞孔更大,吻部更尖;与 *Uralokannemeyeria* 差别在于牙更短小,枕部近于垂直而不是倾斜,头骨背侧后缘为倒 V 字形而不是水平;与 *Rhadiodromus* 相比个体小,眼眶长扁,牙小。Dututt (1989) 根据摩洛哥的材料建立了 *Azarifeneria*,它很不完整,从仅有的材料可以看出其间颞部很宽,与 *Stahleckeria* 很像,不同于新疆的化石。

从以上比较可以看出,新疆的肯氏兽材料是不同于已有属的新类型,故建立新属:

西域肯氏兽(新属) Xiyukannemeyeria **gen. nov.**

词源　西域,化石产地新疆为西域一部分。

特征　见属型种短吻西域肯氏兽。

短吻西域肯氏兽 Xiyukannemeyeria brevirostris **(Sun, 1978)**

特征　中等大小,吻部短且弯曲向下。粗糙面不发育,但有大量纹饰。上颌骨齿突大而厚,牙小。前额骨限于眼眶的前上方,额骨组成眼眶上缘的极大部分。眶后骨向后延伸与鳞骨相接。有前顶骨。间颞区短而较宽。翼骨间孔小。颅基轴平直。枕面不前倾。枕髁分化显著。齿骨缝合部短。隅骨外翼不太向后延伸。肩胛骨无上匙骨沟。

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A NEW MATERIAL OF KANNEMEYERID FROM XINJIANG AND THE RESTUDY OF *PARAKANNEMEYERIA BREVIROSTRIS*

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Key words Turfan, Xinjiang, Middle Triassic, Kelamayi Formation, kannemeyerids

Summary

A new specimen (IVPP V 8311) of kannemeyerid was found in Kelamayi Formation of Turfan, Xinjiang. It is similar to the holotype (IVPP V 4457) of *Parakannemeyeria brevirostris* from Fukang. They share short snout, small tusk, prefrontal only partly entering the orbit, basicranial axis not shortened or curved, occipital condyle with prominent differentiation, but they differ slightly in the intertemporal structure and nasal middle ridge.

The intertemporal structure is one of the important characters used in the classification of dicynodonts. This structure usually varies in different species of one genus in dicynodonts, but if two specimens only differ in intertemporal structure, do they belong to different species? The answer is negative, based on the study of the specimen (IVPP V 4458) from the same locality in Fukang. This specimen includes 9 individuals preserved on one block, they have two different intertemporal structures: the postorbital covers the parietal in the skull of No. 1 (the same as the case in the holotype); the intertemopral region is concave and the parietal is exposed on the skull roof of No. 2～9 (Sun, 1978). In the specimen from Turfan (V 8311) it is the latter case. The specimens V 4458 and V 4457 are regarded as one species despite the difference in the intertemporal region, so is the specimen (V 8311) from Tufan.

There is no nasal middle ridge on specimen V 4457, but it is prominent on specimen V 8311. This character in most skulls of specimen V 4458 is the same as in V 4457. The difference among these skulls could be explained as intraspecies variation.

The specimen V 4457 was named as *Parakannemeyeria brevirostris* by Sun in 1978. Other species in the genera of *Sinokannemeyeria* and *Parakannemeyeria* include: *Sinokannemeyeria pearsoni*, *S. yingchiaoensis*, *S. sanchuanheensis*, *Parakannemeyeria dolichocephala*, *P. youngi*, *P. ningwuensis*, *P. xingxianensis* and *P. shenmuensis* (Young, 1937; Sun, 1960, 1963; Cheng, 1980). *P. xingxianensis*, based on a broken skull, was thought to be *P. ningwuensis* (Sun et al., 1992). In this paper, a cladistic analysis is performed to determine the relationships of these 8 species, using the characters in the skull and lower jaw, rooted on an all-0-outgroup *Dicynodon* (see appendix Ⅰ, Ⅱ for the characters and data matrix). The phylogenetic analysis is done by using the exhausted search of PAUP version 4.0b10 (with all characters unordered). Only one most parsimonious tree is obtained (Fig. 5).

If "*Parakannemeyeria*" *brevirostris* is included in *Parakannemeyeria*, this genus will not be a monophyletic group. So "*Parakannemeyeria*" *brevirostris* should not be referred to this genus. Therefore, "*Parakannemeyeria*" *brevirostris* is also different from other kannemeyerids. So a new genus, *Xiyukannemeyeria* is erected for the specimens from Xinjiang. Its type species is *X. brevirostris*.

The diagnosis of *Xiyukannemeyeria*: skull medium in size; snout short and turned downward; preorbital surface smooth with nasal middle ridge; maxillary process large and thick, tusk small;

prefrontal restricting in anterodorsal corner of the orbit, the frontal forming most part of the dorsal border of the orbit; the postorbital backward to contact with the squamosal; preparietal present; temporal opening short; intertemporal region short and wide; preparietal present; interpterygoid foramen small; basicranial axis not shortened or curved; occipital plate not inclined forward; the symphysis of lower jaw short; the reflected lamina of angular not strongly extending backwards.

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附录 I 用于支序分析的性状

Appendix I The characters used in cladistic analyses

1 skull size: small to medium (0); large (1)

2 skull width in dorsal view: anterior part narrow and posterior part wide (0); both parts are wide (1); both parts are narrow (2)

3 frontonasal area: moderate straight, so the skull is relatively flat (0); curved, so the skull is relatively high (1)
4 ratio of length of preorbital to skull length: less than 40 % (0); more than 45 %(1)
5 ratio of width between orbits to skull length: 40 %～50 % (0); less than 40 %(1)
6 preorbital surface: smooth (0), roughened (1); roughened with pits and striations (2)
7 temporal fenestra: length greater than width (0); width greater or close to length (1)
8 spoon-shaped concave on premaxilla: not present (0); present (1)
9 nasal middle ridge or nasal boss: prominent (0); indistinct (1); not present (2)
10 preparietal: present (0); not present (1)
11 ratio of width of intertemporal region to length of the skull: less than 10 % (0); 10 %～14 % (1); greater than 14 % (2)
12 intertemporal region mainly formed by: postorbital (0); parietal and interparietal (1)
13 maxillary process: small, round (0); large, round (1); large, thin and triangular in lateral view (1)
14 tusk: moderate (0); large (1)
15 posterior part of jugal arch: nearly triangular in cross section (0); dorsal-ventral compressed (1); laterally flattened (2)
16 quadrate ramus of pterygoid: straight posteriorly (0); twisted inwardly (1)
17 groove between basioccipital tuberaes: wide and shallow (0); deep (1)
18 ratio of the height to width of occipital: 50 %～70 % (0); less than 50 % (1); greater than 70 % (2)
19 occipital condyle: prominent differentiation (0); round (1)
20 symphysis of lower jaw: short (0); relatively long (1)

附录 II 性状分布矩阵(? 代表性状缺失)

Appendix II Matrix of taxa and character states (? = information absent)

分类单元	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sinokannemeyeria pearsoni	0	1	0	1	0	1	1	?	1	0	2	0	?	?	1	?	?	1	?	?
Sinokannemeyeria yingchiaoensis	1	1	0	1	0	1	1	0	1	1	2	1	1	0	1	1	0	1	0	1
Sinokannemeyeria sanchuanheensis	0	1	1	0	0	1	1	0	1	0	2	1	1	0	1	1	0	?	0	1
Parakannemeyeria dolichocephala	1	2	1	1	1	2	0	1	2	0	0	0	2	1	2	0	1	2	1	0
Parakannemeyeria youngi	1	0	1	1	1	2	1	1	2	1	0	0	2	1	2	0	1	0	1	0
Parakannemeyeria ningwuensis	1	0	0	1	1	1	1	1	2	0	0	0	0	1	0	0	0	0	0	0
Parakannemeyeria shenmuensis	1	2	1	1	1	1	0	0	2	0	0	1	0	1	2	0	1	2	1	?
“*Parakannemeyeria*” *brevirostris*	0	0	1	0	1	0	0	0	1/2	0	1	0/1	1	0	0	0	0	0	0	0